THE COMPARATIVE MORPHOLOGY OF THE ICACINACEAE
I. ANATOMY OF THE NODE AND INTERNODE

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With four plates

INTRODUCTION

EXTENSIVE INVESTIGATIONS of a wide range of representative dicot-
yledons have demonstrated statistically that the structural specializa-
tions of the cambium and its derivatives tend in general to progress
along a number of clearly defined lines. Not only are these salient
phylogenetic modifications of the cambium and of the secondary xylem
more or less closely correlated, but also at times they synchronize with
morphological specializations of the foliar and floral organs. That they
are significant in discussing the relationships and classification of
families within certain orders of the dicotyledons has been shown by
Vestal (9), Tippo (8) and Taylor (7).

Extensive exploratory investigations have now progressed to a stage
where it becomes desirable to initiate *intensive* studies of specific families.
This is essential in obtaining more detailed information regarding the
relative rates of morphological specializations in different organs and
tissues, in determining which trends of specialization are irreversible,
and in securing clues regarding the actual significance of anatomical
criteria in discussions concerning specific, generic and tribal relationships.

GENERAL PLAN OF PROCEDURE

In the case of most families of the dicotyledons, two types of material
only are available at present for morphological and anatomical investi-
gations, viz. (1) herbarium specimens and (2) the collections of woods
assembled at Yale, Oxford and Harvard Universities and at other insti-
tutions. It is evident, accordingly, that in initiating an intensive study
of a particular family, it is necessary to focus one's attention largely
upon the secondary xylem and upon such tissues and organs as are
adequately preserved in ordinary herbarium specimens, i.e. slender
stems, leaves and flowers.

Our investigations of the Icacinaceae will deal successively with the
gross anatomy of the node and internode, the histology of the tracheary

elements, parenchyma and rays of the cauline secondary xylem, and subsequently with the comparative morphology of the leaves, pollen and flowers. The Icacinaceae were selected for study because they exhibit a wide range of structural specializations and constitute a family that needs critical revision from the taxonomic point of view. Furthermore, the Icacinaceae were differentiated into sub-families and tribes by Engler (1) partly upon the basis of anatomical criteria. Therefore, there is a historical taxonomic precedent for dealing with this family from an anatomical aspect.

The bulk of the putative icacinaceous genera — approximately 60 — has been included in the Icacinoideae. Three genera only are referred to the sub-families Lophopyxidoideae and Cardiopterygoideae. In view of the fact that *Lophopyxis, Cardiopteryx* and *Pteleocarpa* are of questionable icacinaceous affinities, we shall defer consideration of these genera until later and confine our attention for the present to the Icacinoideae.

Our discussions of the vascular structures of this sub-family are based upon the study of 50 genera and of more than 150 species. As will be demonstrated subsequently, such a representation of genera and species is adequate for blocking out the salient lines of structural specializations in the Icacinoideae. Ten genera are not represented in American herbaria. Nor is it possible at present to obtain material of these rarer plants from European collections. Therefore, an analysis of the structure and relationships of these genera must be deferred until suitable material becomes available.

Tribes of the Icacinoideae

According to Engler (1 and 2), there are four tribes of the Icacinoideae which exhibit the following structural and anatomical differences:

1. Icacineae, trees or shrubs, seldom climbers. Vessels with scalariform perforations. Interxylary phloem absent.

2. Iodeae, climbing shrubs, sometimes with tendrils. Vessels with simple perforations. Xylem more prominently developed between the orthostiches of the stem.

3. Sarcostigmateae, climbing shrubs. Vessel elements short with simple perforations. Xylem uniformly developed around the stem. Interxylary phloem present.

4. Phytocreneae, climbing or twining shrubs. Vessel elements short with simple perforations. Xylem prominently developed between the orthostiches. Strands of mixed leptome and hadrome in the orthostiches, rarely continuous around the stem.

This classification of the Icacinoideae attempts to differentiate the anatomically more normal Icacineae from three distinct tribes of climbing plants which exhibit different anomalous modifications of the secondary body. In the case of the Phytocreneae, the so-called strands of mixed leptome and hadrome ("tracheids") actually are secondary phloem which projects into the secondary xylem of young stems of *Phytocrene, Pyrenacantha, Miquelia, Polycephalium* and *Chlamydocarya, Figs. 1 and 2*. These inwardly projecting strands of phloem in the orthostiches fluctuate in number depending upon variations in phyllotaxy, Robinson (3). Compare *Figs. 2 and 3*. They are composed of sieve tubes, companion cells, parenchyma and thick-walled, angular, more or less regularly oriented phloem fibers, *Fig. 4*. In young stems of *Trematosperma cordatum* Urb., as Engler (1) has shown, the strands are more numerous than the orthostiches and do not project conspicuously into the xylem. During subsequent growth of the young stems of *Chlamydocarya Soyauxii* Engl. and *C. Thomsoniana* Baill., they may be occluded in xylem. Such strands of interxylary phloem differ, however, from those of the Sarcostigmateae, *Fig. 10*, by being composed in part of thick-walled fibers, *Fig. 4*.

Although the young stems of the Iodeae, *Figs. 7–9*, may be differentiated from those of the Sarcostigmateae and Phytocreneae by the absence of interxylary phloem and of inwardly projecting strands of hard bast, there is some question whether they can be separated in all cases from those of the Icacineae upon the basis of the anatomical criteria listed by Engler. In the first place, as will be demonstrated in the next paper of this series, a number of the Icacineae are characterized by having vessels with simple porous perforations. In the second place, not all of the Iodeae have as large vessels or as prominently projecting wedges of secondary xylem between the orthostiches of young stems as the species investigated by Robinson (4), Engler (1) and others might lead one to suppose. In the third place, certain representatives of the Icacineae exhibit more or less conspicuous anomalous modifications of the secondary body.

As indicated in *Fig. 13*, the young stems of *Mappianthus iodoides* Hand.-Mazz. exhibit a normal cylindrical development of the secondary body. The vessels are of small size and are more or less uniformly distributed. This is in marked contrast to the conspicuously anomalous structure of such representatives of the Iodeae as *Iodes tomentella* Miq., *Iodes ovalis* Bl., *Fig. 7*, and *Iodes philippinensis* Merr., *Fig. 9*. The young internodes of *Hosiea sinense* (Oliv.) Hemsl. & Wils., *Figs. 5 and 6*, likewise have a normal cylindrical secondary body. In Wilson's material,

the vessels are of small size and are aggregated in three sectors of the secondary xylem, *Fig. 5;* whereas in Yü's specimens, *Fig. 6*, the vessels are relatively large and are more or less uniformly distributed throughout the secondary xylem. *A priori*, such conspicuous structural differences might be interpreted as due to errors in the determination of the specimens. It is significant in this connection, however, that similar structural variations occur in different lateral branches of the same stem of *Iodes liberica* Stapf. Certain of the branches have small vessels as shown in *Figs. 8 and 11;* whereas others have very large ones as illustrated in Fig. 12. Furthermore, the vessels may be uniformly distributed around the stem or may be aggregated in certain sectors of the cross section of the woody cylinder.

In the case of the Icacineae, scandent species of such genera as *Pleurisanthes, Leretia, Lavigeria*, etc., frequently exhibit a tendency to form relatively large vessels which may be aggregated in more or less prominently developed parts of the secondary xylem, i.e., between the orthostiches of young stems. That conspicuously anomalous structures are formed by successive cambia in the older stems of *Lavigeria salutaris* Pierre is indicated in *Fig. 16*. Such facts as these suggest that it may be difficult to differentiate the Iodeae from scandent representatives of the Icacineae upon the basis of Engler's anatomical characterizations of the two tribes.

NODAL ANATOMY

There are three distinct types of nodal anatomy in the stems of dicotyledons. In the *trilacunar* type of node, the vascular supply of the leaf produces three separate gaps in the stele, in the *unilacunar* type, a single gap, and in the *multilacunar* type, more than three gaps. Sinnott (5) has shown that these categories of nodal anatomy are significant in any comprehensive discussion of the relationships and classification of the various families of the dicotyledons. In addition, Sinnott and Bailey (6) have presented evidence which suggests that the primitive nodal condition in dicotyledons is trilacunar. Extensive unpublished investigations of the nodal anatomy of both seedlings and adult plants support this earlier inference, and indicate that the unilacunar condition arises from the trilacunar by the suppression of its lateral traces and corresponding gaps. The multilacunar condition develops from the trilacunar by the addition of successive pairs of lateral traces and gaps.

Although the finer details of the nodal structure of the Icacinaceae will be discussed later in connection with the leaf, it is advisable at this

point to emphasize the fact that the Icacinoideae may be divided into two distinct sections upon the basis of salient features of their nodal anatomy. One section of the sub-family is characterized by having trilacunar nodes, *Fig. 14,* and the other section by its unilacunar ones, *Figs. 1 and 15.* The multilacunar condition is not encountered in any of the Icacinoideae that we have studied.

TRILACUNAR — ICACINOIDEAE

ICACINEAE

Anisomallon	Dendrobangia	Lasianthera	Pittosporopsis
Apodytes	Discophora	Leptaulus	Platea
Calatola	Emmotum	Medusanthera	Poraqueiba
Cantleya	Gastrolepis	Oecopetalum	Stemonurus
Cassinopsis	Gonocaryum	Ottoschulzia	Urandra
Citronella	Grisollea	Pennantia	

UNILACUNAR — ICACINOIDEAE

ICACINEAE

Alsodeiopsis	Lavigeria	Merrilliodendron
Desmostachys	Leretia	Pleurisanthes
Humirianthera	Neoleretia	Rhaphiostylis
Icacina	Mappia	Rhyticaryum

IODEAE

Hosiea	Natsiatum	Mappianthus
Iodes	Polyporandra	

SARCOSTIGMATEAE
Sarcostigma

PHYTOCRENEAE

Chlamydocarya	Polycephalium
Miquelia	Pyrenacantha
Phytocrene	

It is evident from this tabulation of genera that there is one section of the Icacineae which resembles the Iodeae, Sarcostigmateae, and Phytocreneae in having unilacunar nodes. Furthermore, it is signifi-cant that a truly scandent habit of growth rarely, if ever, occurs among the trilacunar representatives of the Icacineae. On the contrary, several genera of the unilacunar Icacineae exhibit an evident tendency towards the acquisition of a scrambling, twining or climbing habit. This sug-gests that certain of the unilacunar Icacinaceae may be transitional in form and structure between the non-scandent, trilacunar Icacineae and

the unilacunar Iodeae, Sarcostigmateae and Phytocreneae in which a twining or climbing habit of growth is dominant. Such a supposition is strengthened by a study of the vessels of the Icacinoideae which will be discussed in the second paper of this series.

SUMMARY

1.   The reasons for initiating an intensive study of the comparative morphology of the Icacinaceae are presented.

2.   The general plan of procedure in this series of investigations is briefly outlined.

3.   Engler's anatomical characterizations of four tribes of the Icacinoideae are discussed and the question is raised whether the Iodeae can be differentiated in all cases from the Icacineae by the suggested anatomical criteria.

4.   A study of the nodal anatomy of the Icacinoideae reveals the fact that there are two distinct categories of the Icacineae, (1) those characterized by trilacunar nodes and (2) those having unilacunar ones.

5.   Certain of the unilacunar Icacineae appear to be somewhat transitional in form and structure between the non-scandent, trilacunar Icacineae and the unilacunar Iodeae, Sarcostigmateae, and Phytocreneae in which a twining or climbing habit of growth is dominant.

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ing the relationships of the Hypericaceae to the Guttiferae and their
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DESCRIPTION OF PLATES

Plate I

Fig. 1. *Chlamydocarya capitata* Baill.,   *Linder 1076.*
Transverse section of the node.   The vascular tissues of the
leaf at (m) produce a single gap in the stele. $\times$ 14.

Fig. 2. *Chlamydocarya capitata* Baill.,   *Linder 1076.*
Transverse section of the internode, showing five wedges of large-
vesselled secondary xylem and five strands of hard bast, correlated
with a 2/5 phyllotaxy. $\times$ 11.

Fig. 3. *Pyrenacantha repanda* Merr.,   *Wenzel 2607.*
Transverse section of a stem having 1/3 phyllotaxy.   The three
arcs of large-vesselled xylem and the three strands of hard bast
are separated from the internal primary body by a nearly normal
cylinder of secondary xylem. $\times$ 22.

Fig. 4. *Chlamydocarya capitata* Baill.,   *Linder 1076.*
Transverse section of a strand of secondary phloem, showing sieve
tubes and thick-walled fibers. $\times$ 90.

Fig. 5. *Hosiea sinense* (Oliv.) Hemsl. & Wils.,   *Wilson 960.*
Transverse section of a stem, showing four growth zones of small-
vesselled secondary xylem. $\times$ 16.

Fig. 6. *Hosiea sinense* (Oliv.) Hemsl. & Wils.,   *Yü 1932.*
Transverse section of a stem, showing four growth zones of
large-vesselled secondary xylem. $\times$ 16.

Plate II

Fig. 7. *Iodes ovalis* Bl.,   *H. U. 2775-J.**
Transverse section of the stem, showing "anomalous" develop-
ment of large-vesselled secondary xylem. $\times$ 8.

Fig. 8. *Iodes liberica* Stapf.,   *Linder 1102.*
Transverse section of a stem, showing somewhat asymmetrically
developed small-vesselled secondary xylem. $\times$ 25.

Fig. 9. *Iodes philippinensis* Merr.,   *Philip. Bur. Sci. No. 987.*
Transverse section of a stem, showing "anomalous" development
of large-vesselled secondary xylem. $\times$ 25.

Plate III

Fig. 10. *Sarcostigma Horsfieldii* R. Br.,   *H. U. 2771-J.*
Transverse section of the xylem, showing included strands of soft
bast. $\times$ 50.

Fig. 11. *Iodes liberica* Stapf.,   *Linder 1102.*
Transverse section of *Fig. 8* more highly magnified. $\times$ 50.

*The numbers *H. U. 2775-J* and *H. U. 2771-J* refer to specimens in the wood
collection at Harvard University.

FIG. 12. *Iodes liberica* Stapf., *Linder 1102*.
Transverse section of another part of the same stem, showing large-vesselled secondary xylem. × 50.

PLATE IV

FIG. 13. *Mappianthus iodoides* Hand.-Mazz., *How 72874*.
Transverse section of a stem, showing normal development of the secondary xylem. × 20.

FIG. 14. *Citronella sarmentosum* (Baill.) Howard, *Bonati 1113*.
Transverse section of a node showing trilacunar condition. Median trace and gap at (m). Lateral traces and gaps at (1). × 22.

FIG. 15. *Lavigeria salutaris* Pierre, *Milbraed 10536*.
Transverse section of the node and the base of the petiole, showing unilacunar condition at (m). × 13.

FIG. 16. *Lavigeria salutaris* Pierre, *Milbraed 10536*.
Transverse section of an older stem, showing "anomalous" structure formed by successive cambia. × 16.

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